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Immobilization and bacterial utilization of dissolved organic carbon entering the riparian zone of the alpine Enns River, Austria

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ABSTRACT: In order to understand the factors controlling the removal of riverine dissolved organic carbon (DOC) in the riparian zone of an alpine river, concentrations of DOC and dissolved oxygen, as well as bacterial abundance and production, were determined in interstitial waters of an experimental bank filtration site of the Enns River, Austria. Four porewater stations exhibiting differing sedimentologic and hydrologic characteristics were sampled over an annual cycle. We found that concentrations of DOC, oxygen, bacterial biomass and production decreased significantly within the first meter from the sediment-water interface. Differences in the grain size distribution among the sampling stations led to spatial heterogeneity in the permeability of the riparian sediments and in the hydraulic residence time of the infiltrating river water, resulting in specific patterns in DOC immobilization and microbial respiration. Porewater bacterial abundance and production and apparent microbial oxygen consumption were positively correlated with the hydraulic residence time of the infiltrating water. DOC occasionally accumulated in the shallow porewater layers during the winter. During the summer, DOC infiltrating from the river surface potentially explained only 36 ± 25% of the apparent interstitial oxygen consumption. This suggests that particulate organic carbon (POC) contributes substantially to the microbial organic carbon supply in the hyporheic zone. We conclude that the availability of POC rather than DOC infiltration determines hyporheic microbial metabolism.

KEY WORDS: Hyporheic bacteria · POC · DOC · Respiration · Sediment · Bank filtration · Enns River

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INTRODUCTION

Hyporheic ecotones play a crucial role in the functioning of lotic ecosystems (Brunke & Gonser 1997). On the one hand, hyporheic processes control the exchange of water and solutes between the rivers and streams and the adjacent groundwater and may partially determine the distribution and supply of nutrients within the lotic system (Vervier et al. 1993, Findlay & Sobczak 1996, Valett et al. 1997). On the other hand, hyporheic habitats are important storage zones for organic carbon (Leichtfried 1991, Bretschko & Moser 1993) and are generally characterized by sharp physical and chemical gradients (Hendricks & White 1995, Fraser & Williams 1998), thus enabling a broad spectrum of metabolic pathways to occur within small spatial scales. As a consequence, hyporheic habitats are often hot spots in productivity and diversity of organisms (Pusch et al. 1998) and may contribute substantially to the energy flow through the lotic system (Jones & Holmes 1996, Naegeli & Uehlinger 1997, Romaní et al. 1998).

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Because primary production in interstitial habitats is limited to the surface layers, hyporheic heterotrophic microorganisms largely depend on the input of organic carbon and energy from allochthonous sources. Dissolved organic matter (DOM) may be imported from surface water (Findlay et al. 1993, Mann & Wetzel 1995, Findlay & Sobczak 1996) or groundwaters (Ford & Naiman 1989, Fiebig & Lock 1991, Kaplan & Newbold 1993, Schindler & Krabbenhoft 1998). In addition, particulate organic matter (POM) can be an important carbon source especially in shallow sediment layers (Brunke & Gonser 1997) and might control hyporheic microbial metabolism (Hedin 1990, Sobczak et al. 1998). Overall, the extent of hydrologic interaction between surface water and groundwater and the direction of the interstitial flow (i.e. upwelling vs downwelling) are major factors controlling the availability of oxygen and nutrients and, therefore, the biological activity in hyporheic habitats (Hendricks 1993, Findlay 1995, Valett et al. 1997).

The chemical and biological characteristics of downwelling surface water change significantly upon subsurface transport (Hoehn et al. 1983, Hendricks & White 1995, Marmonier et al. 1995). In particular, dissolved oxygen and dissolved organic carbon (DOC) have been demonstrated to decline along interstitial flow paths (Findlay et al. 1993, Hendricks 1993, Findlay & Sobczak 1996). The removal of DOC from porewater takes place via a combination of abiotic and biotic processes (Fiebig & Marxsen 1992) and is mainly associated with sediment biofilms (Lock et al. 1984, Freeman et al. 1995). Among biofilm organisms, heterotrophic bacteria represent a significant biomass component and may be responsible for a major part of the system's respiration (Pusch 1996). Uptake and incorporation of DOC into bacterial biomass is a key process in the potential transfer of DOC to higher trophic levels of the hyporheic food web (Meyer 1994).

The importance of subsurface zones for the processing of organic carbon and nutrients and the implication of such processes for river restoration has been recognized (e.g. Vervier et al. 1993, Brunke & Gonser 1997). In addition, the transport of surface water through the riparian zones of rivers and lakes by artificial means (bank filtration) has become increasingly important for drinking water production, because organic matter as well as pollutants and harmful bacteria potentially present in the infiltrating water are efficiently retained during transport through the river bank (Schwarzenbach et al. 1983, Marmonier et al. 1995, Freedman et al. 1997).

Brugger et al. (in press) investigated a series of porewater and sediment stations from an experimental bank filtration site at the Enns River (Upper Austria) and found oxygen concentration, particulate organic carbon (POC) concentration, and bacterial abundance and production to decrease with increasing lateral distance from the river. The steepest gradients were observed within the first meter from the sediment-water interface (Brugger et al. in press). Immobilization of DOC was less pronounced and mainly due to abiotic mechanisms (Kolar et al. unpubl.). These findings support earlier reports (Hoehn et al. 1983, Marmonier et al. 1995) pointing to the importance of shallow subsurface layers in modifying the quality of the infiltrating waters. In the present paper, we therefore specifically focus on the dynamics of dissolved oxygen, DOC, and bacteria in the shallow riparian porewater (<1 m from the sediment-water interface). We tested the effect of specific geohydrologic properties of the riparian surface sediments on the removal of DOC and oxygen from the infiltrating water and assessed the importance of DOC versus POC for the metabolism of the hyporheic microbial community. Furthermore, the significance of porewater bacteria versus sediment-attached bacteria was evaluated.

MATERIALS AND METHODS

Study location. The Enns River is a mesotrophic alpine river originating in the Austrian Central Alps and entering the Danube River (inset in Fig. 1). Catchment geology and hydrographic characteristics of the Enns River have been described previously (Brugger et al. in press). Sampling was carried out at an experimental bank filtration site located on the left bank of the Garsten impounding reservoir, about 10 km south of the town of Steyr (47° 59′ N, 14° 22′ E). Infiltration of surface water into the riverbank was mediated by pumping from a water production well located about 50 m from the riverbank (Fig. 1). This well was put in operation on 14 October 1997. As a consequence, the direction of interstitial flow switched from a slight outflow of hyporheic groundwater (Ennskraft Inc., Dept. Technical Services, unpubl. data) to influx of river water into the riparian zone (Fig. 2, Table 1). The production rate of the well was set at 0.02 m^3 s^{-1} and remained constant throughout the study period (October 1997 to September 1998).

At the study site, the aquifer material consists of a 5 to 10 m thick layer of calcareous glacial gravel deposits overlaying an impermeable layer of flysch (Fig. 1). Grain size analyses of the bank sediments (collected from 0 to 2 m depth) were performed at the beginning of the study and revealed a mean particle size distribution of 50% gravel, 35% sand, 15% silt, and 5% clay. Higher proportions of silt and clay (up to 35%) were found near the sediment-water interface (K.-H. Steiner & E. Mekonen unpubl. data).

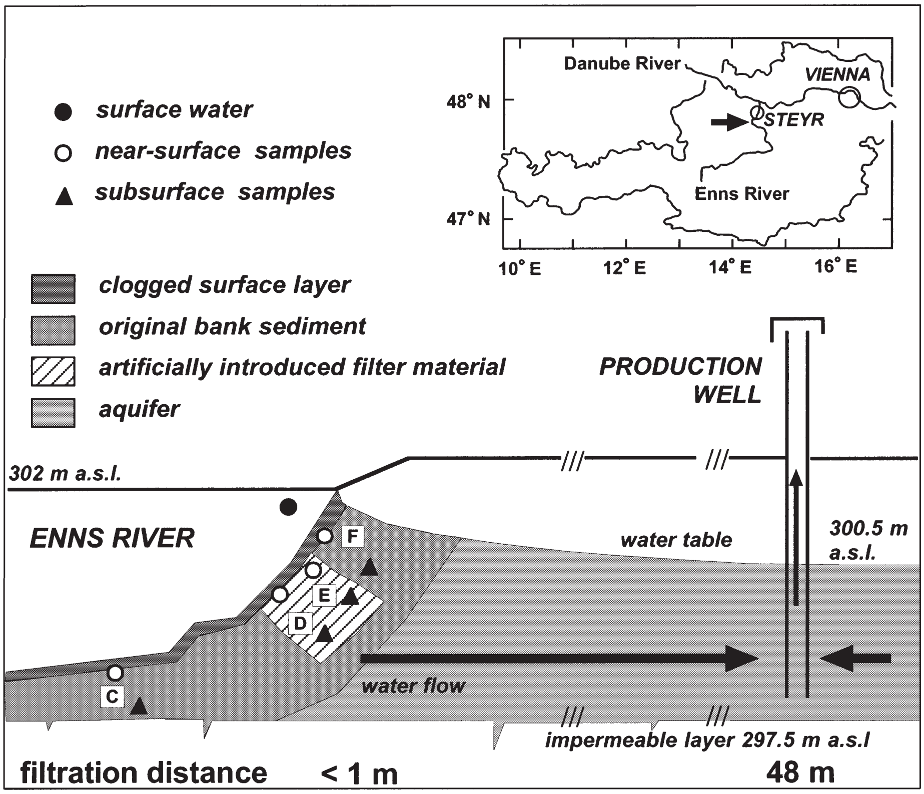

Fig. 1. Schematic cross-sectional view of the sampling site with production well, positions of the sampling points, and general geohydrologic compartments. Stns C and F were deployed in undisturbed sediments, while Stns D and E were embedded in artificially introduced filter material (grain diameter: 4 mm). Symbols represent the sampling site in the river channel (●) and in the near-surface (O) and subsurface (▲) sediment layers. For details see 'Materials and methods'. a.s.l.: above sea level

Porewater samples were taken from 4 different locations (Fig. 1): Stn C was located in the transition zone between the riverbed and the riverbank. Stn F was located on the riverbank, 0.5 to 1.5 m below the mean water level of the Enns River. Two additional sampling stations (Stns D and E) were also located on the riverbank, about 3 m downstream of Stn F, and covered a region where defined filter material had been introduced into the bank 4 mo before the beginning of this study. This defined material, consisting of calcareous gravel, was sieved and washed to obtain a mean grain diameter of 4 mm.

Field methods. Each sampling station consisted of a pair of piezometer wells (perforated metal pipes with 10 mm inner diameter), which allowed one to determine the vertical hydraulic gradients (VHG) and hydraulic conductivity as well as to sample interstitial water. The positions of the individual sampling points were located at the following depths below the sediment-water interface: 0.2 and 0.9 m (Stn C); 0.1 and 1.0 m (Stn D); 0.3 and 0.9 m (Stn E); and 0.1 and 0.9 m (Stn F) (Fig. 1). For comparisons between sites, the sampling points are grouped in 'near-surface' (0.1 to 0.3 m) and 'subsurface' samples (0.9 to 1.0 m from the sediment surface).

VHG were determined about once a week throughout the investigation period. VHG were defined as the difference in hydraulic head between the river channel and the interstitial water divided by the depth of the piezometer (Lee & Cherry 1987). Negative VHG values indicate infiltration of surface water into the riparian sediments. Hydraulic conductivity (*kf*-values) was measured at Stns D and F using falling head tests (Lohr 1969). Measurements of *kf* were performed on 4 dates (20 October 1997, 10 November 1997, 18 May 1998, and 29 September 1998).

Temperature, concentrations of oxygen and DOC, and bacterial parameters (abundance and production) were determined at monthly intervals. Interstitial water (about 100 ml) was carefully withdrawn from each pipe and temperature and oxygen concentration were measured immediately using combined electrodes (WTW, Germany). Subsequently, water samples were placed into acid-rinsed and combusted (450°C, 6 h) glass vials and stored in the dark at 4°C until further processing (within 12 h). Subsamples for bacterial abundance were preserved immediately with 2% formaldehyde (final concentration).

Measurements performed in the laboratory. DOC concentrations were measured on a Shimadzu TOC-5000 analyzer (Benner & Strom 1993). Before analysis, samples were filtered through combusted (450°C, 6 h) Whatman GF/F filters. The DOC content was determined after sparging the samples with CO_2-free air.

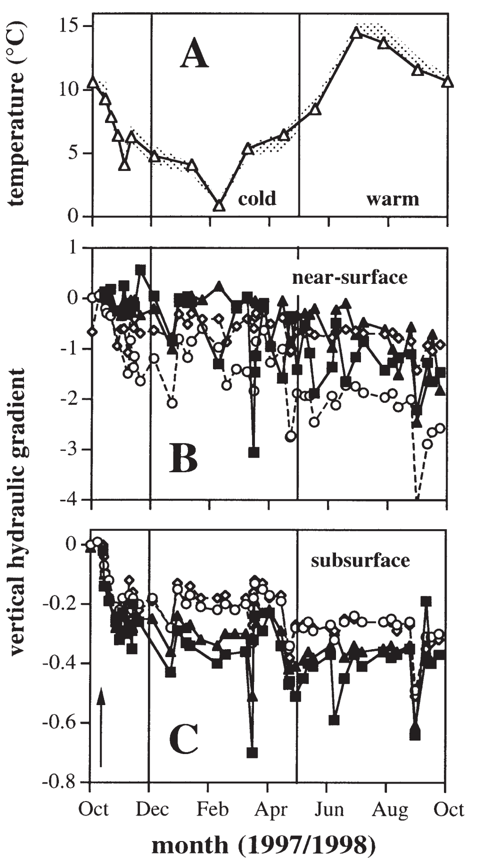

Fig. 2. (A) Seasonal variation in temperature in the surface waters of the Enns River (▲) and at the riparian porewater stations (shaded area); (B) time course of the vertical hydraulic gradient (VHG) between the river channel and the porewater sampling points for the near-surface layer, and (C) for the subsurface layer. Symbols represent Stns C (■), D, (O), E (◇), and F (▲). The arrow in (C) refers to the beginning of pumping activity from the well on 14 October 1997

Table 1. Summary of geohydrologic characteristics from 2 stations of the investigated riverbank at Stns D and F. Hydraulic conductivity (*kf*), filtration velocity (*v*), and hydraulic residence time (HRT) were calculated for the shallow riparian zone (between the sediment-water interface and subsurface sediment layers; see Fig. 1)

Date	*kf* ($\times 10^{-5}$ m s^{-1})	*v* ($\times 10^{-5}$ m s^{-1})	HRT (d)
Stn D			
20 Oct 1997	9.66	2.06	0.56
10 Nov 1997	5.17	2.27	0.51
18 May 1998	4.16	1.77	0.65
29 Sep 1998	3.94	1.87	0.62
Stn F			
20 Oct 1997	4.27	1.01	1.03
10 Nov 1997	2.45	1.23	0.85
18 May 1998	0.32	0.15	6.75
29 Sep 1998	1.75	0.93	1.13

Standards were prepared with potassium hydrogen biphthalate (Kanto Chemical Co Inc.). The blank was, on average, ~15.2 ± 7.7 µM C (range 5 to 32 µM C) and the average analytical precision of the instrument was <4%. At least triplicate measurements per sample were performed.

Bacterial numbers were determined using DAPI staining and epifluorescence microscopy (Porter & Feig 1980). At least 300 cells were enumerated per filter and sample. Bacterial production (BP) was measured via the incorporation of ^{3}H-labelled leucine (specific activity: 120 Ci mmol^{-1}; Amersham) into bacterial protein (Simon & Azam 1989). Water samples were amended with 10 nM (final concentration) leucine and incubated for 1 h. All measurements were performed at near *in situ* temperature in triplicate with 1 formaldehyde-killed control. After the incubation, the samples were collected on filters and the radioactivity was determined in a scintillation counter (Canberra-Packard, TriCarb 2000). Bacterial carbon production was calculated from leucine incorporation using the equations given in Simon & Azam (1989).

Calculations. Infiltration velocities (v) were determined using Darcy's equation as $v = dh/dl \times kf$, where (dh/dl) is the VHG between near-surface and subsurface sampling points and *kf* is the average hydraulic conductivity within this layer (Lee & Cherry 1987). The hydraulic residence time of the infiltrating water within the upper meter of the riparian zone was calculated based on a mean sediment porosity of 20% (Ingerle et al. 1999).

DOC immobilization (ΔDOC; sensu Fiebig & Marxsen 1992) upon transport of river water through the top meter of the riparian zone was defined as the difference in DOC concentration between river water and the depths of the respective sediment layer. Similarly, the apparent oxygen consumption (ΔO_2) upon filtration was calculated as the difference in oxygen concentration between river water and interstitial water collected in the respective sediment layer. ΔDOC and ΔO_2 are expressed in µmol C l^{-1} and µmol O_2 l^{-1}, respectively.

In order to evaluate the role of surface-derived DOC for the metabolism of the interstitial microbial community, ΔO_2 was converted into loss of organic carbon due to microbial respiration (hyporheic carbon respiration, HCR). HCR (in µmol C l^{-1}) was calculated as $\Delta O_2 \times 0.85$; 0.85 was used as the respiratory quotient (Fischer et al. 1996 and references therein).

Statistical analyses. Differences between sample means were tested for significance using analysis of variance (ANOVA), if conditions for parametric methods were met; otherwise, Friedman's test was used. Grouping variables were: station (Stns C, D, E and F), sediment depth ('near-surface', 'subsurface') and season ('cold', i.e. December 1997 to April 1998; 'warm', i.e. May to September 1998). Post-hoc comparisons were performed using Scheffe's test (SAS Institute Inc. 1998). Respective losses of DOC and oxygen were compared using Student's *t*-tests. Relationships between the parameters were examined using Pearson's correlation coefficient. Multiple regression models were applied to predict losses of DOC and oxygen during filtration.

All statistical analyses were performed using the SAS StatView 5.0 software. Log-transformation was used to normalize data. Homogeneity of variance among sample means was confirmed using Bartlett's test (SAS Institute Inc. 1998).

RESULTS

Temperature regime

In the river, water temperature showed a marked seasonality ranging between 0.9°C (9 February 1998) and 14.5°C (29 June 1998; Fig. 2A). The temperature of the porewater strongly followed the seasonal pattern observed in the river channel (r always > 0.95; n = 23; p < 0.001), with similar interstitial temperatures at all stations and sediment layers. Consequently, no significant differences in temperature between stations or depth layers were detectable (2-way ANOVA; p > 0.05).

Vertical hydraulic gradient and hydraulic conductivity

The seasonal patterns of the VHG between the river channel and the porewater stations (Fig. 2B,C) illustrate the shift in the direction of the interstitial flow at the beginning of the investigation period. As pumping was started (on 14 October 1997), VHG generally turned from slightly positive values to negative values. Especially in the near-surface sediment (0.1 to 0.3 m depth; Fig. 2B), VHG was affected by fluctuations of the river water table elevation (r always > 0.70; n = 42; p < 0.001). Despite these short-term fluctuations, however, VHG steadily increased at all stations over the investigation period (indicated by more negative values). VHG was much steeper in near-surface sediment layers (Fig. 2B) than in the subsurface layers and was most pronounced at Stn D (Fig. 2C). In the subsurface layers, VHG was significantly higher at stations with natural filter material than at stations with artificially introduced filter material (Fig. 2C, Table 2). During the warm season, VHG was most pronounced at Stn C (Table 2).

Table 2. Friedman-test on differences between stations (Stns C, D, E and F) in vertical hydraulic gradient (VHG), concentrations of DOC and oxygen, and bacterial parameters (abundance [BA] and production [BP]). Data were log-transformed before analysis and grouped according to depth layer and season; see 'Materials and methods' section). df = 3; –: not determined (due to missing values); ⇔ denotes significant differences between stations in post-hoc comparison (using Scheffé's repeated measures design; α = 0.05)

Parameter	Depth layer	Season	n	χ^2	p	Post-hoc groups
VHG	Near-surface	Cold	26	45.554	<0.001	D ⇔ CEF
		Warm	16	34.425	<0.001	D ⇔ CEF
	Subsurface	Cold	26	53.765	<0.001	CF ⇔ DE
		Warm	16	35.175	<0.001	C ⇔ DE ⇔ F
DOC	Near-surface	Cold	5	7.980	0.046	C ⇔ DEF
		Warm	5	1.140	0.767	
	Subsurface	Cold	5	5.040	0.169	
		Warm	5	10.260	0.017	C ⇔ DEF
Oxygen	Near-surface	Cold	5	9.780	0.021	C ⇔ DEF
		Warm	5	8.280	0.041	C ⇔ E
	Subsurface	Cold	5	14.460	0.002	C ⇔ DE
		Warm	5	12.064	0.007	C ⇔ DF ⇔ E
BA	Near-surface	Cold	5	13.560	0.004	CF ⇔ DE
		Warm	3	–	–	C ⇔ DE ⇔ F
	Subsurface	Cold	5	4.920	0.178	
		Warm	5	4.938	0.286	
BP	Near-surface	Cold	5	8.760	0.033	CF ⇔ DE
		Warm	5	12.120	0.007	CF ⇔ DE
	Subsurface	Cold	5	11.880	0.008	C ⇔ DEF
		Warm	5	10.860	0.012	C ⇔ DEF

The *kf*-values obtained for Stns D and F (Table 1) provide an explanation for the observed patterns in VHG (shown in Fig. 2). Hydraulic conductivity was significantly lower at Stn F than at Stn D (paired *t*-test; $p < 0.05$), presumably caused by the higher proportion of fine particles present at the undisturbed sites than at sites with artificially introduced filter material. Infiltration velocity at Stn D was always at least twice as high as at Stn F (Table 1).

Dynamics of DOC and dissolved oxygen in the riparian porewater

Due to the pumping activity, hyporheic porewater was replaced by water infiltrating from the river. This resulted in considerable changes in porewater chemistry within 1 mo (from October to November 1997) after pumping from the well had started, which also affected the distribution of organic carbon and the microbial metabolism within the shallow hyporheic zone. In the following we focus on the dynamics of DOC and dissolved oxygen between December 1997 and September 1998, when river water predominated at all sampling sites (Brugger et al. in press).

The concentration of river DOC remained relatively stable over the investigation period (mean ± SD: 89 ± 14 µmol C l^{-1}; n = 10) but tended to decline towards the summer (Fig. 3A). A pronounced peak (179 µmol C l^{-1}) was detected on 27 July 1998, coinciding with enhanced precipitation prior to the sampling date. The porewater DOC concentrations followed the seasonal pattern observed in the river channel but were generally lower than the corresponding river values. At Stns D, E, and F, decreases in DOC concentration were detectable mainly between the sediment-water interface and the near-surface layers (paired *t*-test; $p < 0.01$). No significant further DOC decline was detectable between the near-surface and subsurface sediment layers except for Stn C, where DOC concentrations significantly declined between these layers (paired *t*-test; $p < 0.01$). The overall DOC loss within the top meter of filtration was therefore higher at Stn C (33 ± 10% of the river DOC concentration; n = 10) than at the other stations (15 ± 13%, n = 10; Fig. 3A).

In the river water, oxygen concentrations were highest in Febrary (411 µmol O_2 l^{-1}) and decreased afterwards until the end of the study (Fig. 3B). The lowest oxygen concentration was measured in August (295 µmol O_2 l^{-1}). Oxygen saturation in the river averaged 93 ± 5% (n = 10) over the investigation period, with no significant difference detectable between seasons (ANOVA; $p > 0.05$). During the winter, interstitial oxygen concentration declined only slightly with depth, especially at locations with artificially introduced gravel (Stns D and E). Oxygen concentration decreased only by 5 ± 3% at Stn D and by 3 ± 2% at Stn E over the first meter of filtration. Significantly steeper O_2 gradients were observed at Stn C (22 ± 10%) and at Stn F (13 ± 10%; Table 2). During the summer, oxygen concentration generally declined more rapidly with depth (Fig. 3B). Again, oxygen decline was highest at Stns C (42 ± 11% the respective river values) and F (39 ± 13%), followed by Stns D (29 ± 10%) and E (14 ± 7%).

Interstitial bacterial abundance and production

Riverine bacterial abundance displayed a pronounced seasonal dynamic, with lowest numbers ($\approx 5 \times 10^8$ cells l^{-1}) from Febrary through April 1998 and highest numbers (16×10^8 cells l^{-1}) in June and July 1998 (Fig. 3C). Site-specific differences in bacterial abundance were discernible for the near-surface layer (Table 2). At locations with artificially introduced gravel (Stns D and E), bacterial abundance declined sharply with depth (paired *t*-test; $p < 0.001$) to about 30% of the corresponding river values, with only minor seasonal variation ($2 \pm 1 \times 10^8$ cells l^{-1}). In contrast, the near-surface sediment layers of Stns C and F showed much higher seasonal variations, following the pattern observed in the river channel (Fig. 3C). Both stations showed similar bacterial numbers ($6 \pm 2 \times 10^8$ cells l^{-1}) during the cold season, whereas, during the summer, bacterial abundance was significantly higher at Stn C ($13 \pm 3 \times 10^8$ cells l^{-1}) than at Stn F ($6 \pm 3 \times 10^8$ cells l^{-1}; Table 2). In the subsurface layer (at 0.9 to 1 m distance from the river water-sediment interface), porewater bacterial abundance was significantly lower than in the river channel (paired *t*-test; $p < 0.001$) and averaged $1.7 \pm 0.9 \times 10^8$ cells l^{-1}, with no significant differences discernible among stations (Table 2).

Porewater bacterial production followed a seasonal pattern that differed considerably from that observed for the river (Fig. 3D). Significant differences were also observed between locations with natural filter material and artificially introduced filter material (Table 2). At Stns D and E (with artificially introduced gravel), bacterial production was generally lower than in the river, with no significant differences detectable between the 2 stations and the 2 depth layers (2-way ANOVA; $p > 0.05$). In contrast, at Stns C and F, near-surface bacterial production was significantly (up to 20 times) higher (paired *t*-test; $p < 0.01$) than in the river, with maximum production rates measured in January (0.8 to 0.9 µmol C l^{-1} d^{-1}) and in June (1.4 µmol C l^{-1} d^{-1}). In the subsurface layer, Stn C displayed significantly higher bacterial production rates than any other location (Table 2).

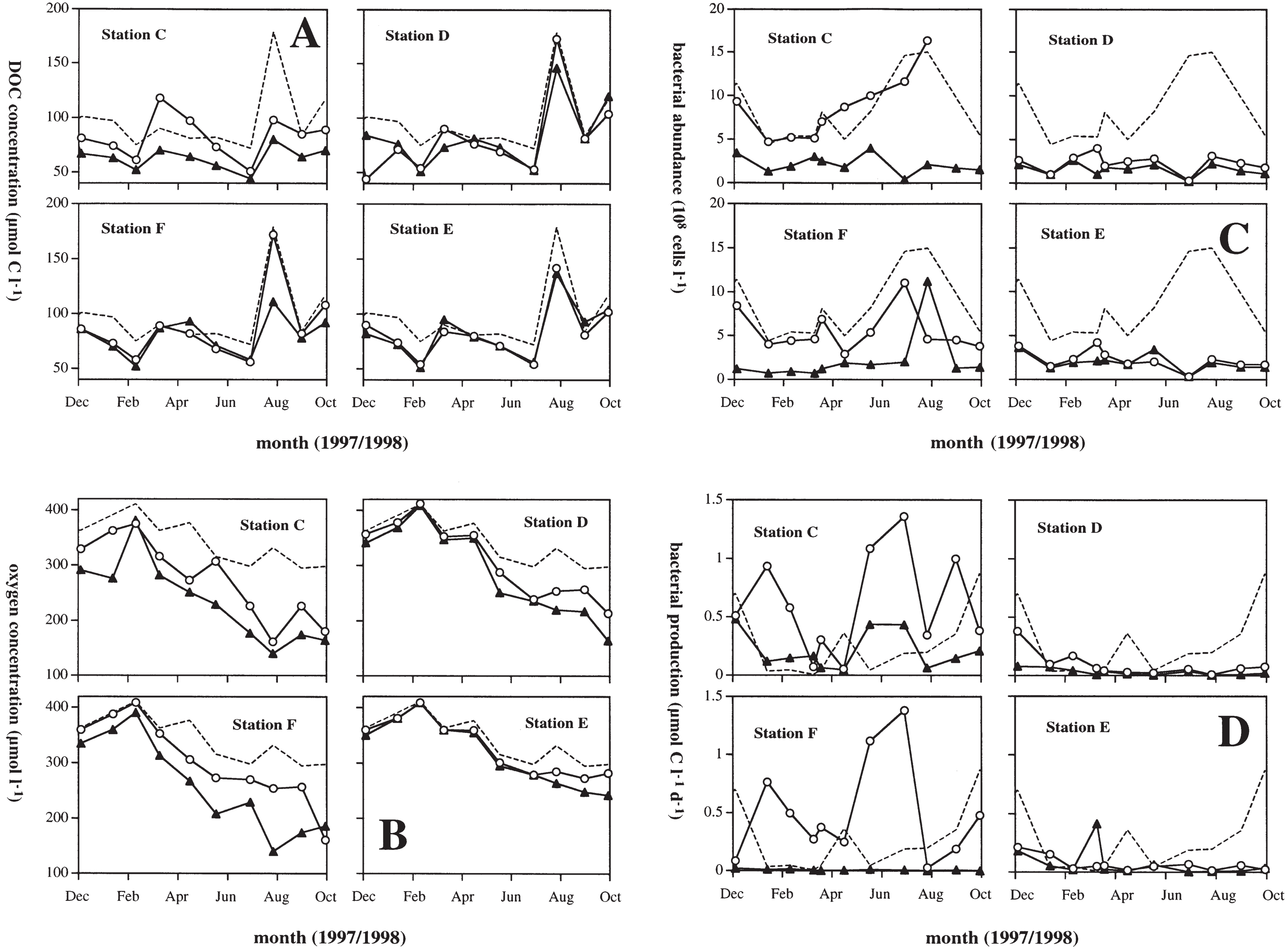

Fig. 3. Seasonal variation of (A) DOC concentration, (B) oxygen concentration, (C) bacterial abundance, and (D) bacterial production at the 4 riparian porewater stations and, for comparison, in the Enns River (broken line). (O) Near-surface sediment layer; (▲) subsurface sediment layer (for details on the position of the stations see Fig. 1)

Table 3. Pearson's correlation coefficients between temperature, vertical hydraulic gradient (VHG), concentrations of DOC and oxygen, and bacterial abundance (BA) and production (BP) in the riparian porewater; n = 80 (BA: n = 78). Levels of significance: *p < 0.05; **p < 0.01; ***p < 0.001

	Temperature	VHG	DOC conc.	Oxygen conc.	BA
VHG	−0.303**				
DOC conc.	0.333**	−0.111			
Oxygen conc.	−0.798***	0.218	−0.258*		
BA	0.070	−0.143	0.138	−0.082	
BP	0.048	−0.094	−0.248*	−0.003	0.593***

Interaction between bacterial abundance and production and physical and chemical parameters

Bacterial variables were only weakly related to the measured physical and chemical parameters. When data from all stations and depth layers were pooled, neither temperature, VHG, or concentrations of DOC and oxygen correlated with bacterial abundance (Table 3), and only DOC concentration correlated weakly with bacterial production ($r = -0.248$; $p < 0.05$; Table 3). However, bacterial abundance was significantly correlated with temperature ($r = 0.878$; $p < 0.01$) and oxygen concentration ($r = -0.892$; $p < 0.01$) in the near-surface layer of Stn C. Similarly, a relationship between bacterial production and DOC concentration was obtained ($r > 0.600$; $p < 0.05$) if only data from the near-surface layers were considered. Pooling all the stations and depth layers, bacterial abundance was significantly correlated with production ($r = 0.593$; $p < 0.001$; Table 3).

DOC immobilization and hyporheic carbon respiration in the riparian zone

Over the first 0.9 to 1 m of water transport, DOC immobilization (ΔDOC; Fig. 4) varied irregularly between seasons (ANOVA; $p > 0.05$), but was significantly higher at Stn C (35 ± 24 µmol C l^{-1}) than at any other sampling station (15 ± 16 µmol C l^{-1}; Scheffé's post-hoc comparison; $p < 0.05$). The decline in DOC over the top meter layer was highest in July, coinciding with highest DOC concentrations in the river (Fig. 3A). Hyporheic carbon respiration (HCR; calculated from the apparent oxygen consumption) was low from December through February and increased with increasing temperature towards the summer (Fig. 4). HCR was highest at Stns C and F (overall mean ± SD: 92 ± 16 and 72 ± 46 µmol C l^{-1}, respectively). Significant differences were detected also between Stns D (46 ± 37 µmol C l^{-1}) and E (22 ± 19 µmol C l^{-1}; Scheffé's post-hoc test).

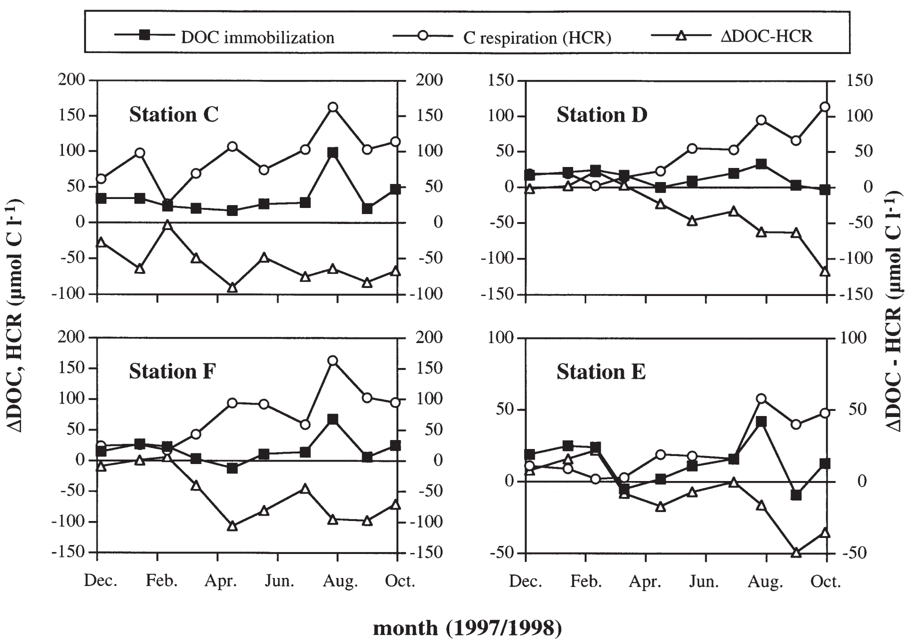

Fig. 4. Seasonal variation of DOC immobilization (ΔDOC), total hyporheic carbon respiration (HCR), and the difference between ΔDOC and HCR (ΔDOC – HCR) in the riparian zone (within 0.9 to 1 m from the sediment-water interface). Note different scales on *y*-axes

Higher ΔDOC than HCR values in Fig. 4 indicate accumulation of DOC within the sediment, while ΔDOC < HCR indicates the amount of organic carbon respired which cannot be explained by the observed loss of DOC. The magnitude of the imbalance between ΔDOC and HCR varied significantly between stations and seasons (2-way ANOVA; $p < 0.05$ and $p < 0.001$, respectively). At Stn C, HCR was always higher than ΔDOC (paired *t*-test; $p < 0.001$). Microbial DOC mineralization could account for, at most, 45 ± 26 % of the apparent oxygen consumption, assuming that no abiotic loss of DOC from the porewater took place. The stations located farther along the riverbank were characterized by occasional accumulation of DOC during the winter (especially at Stns D and E, where ΔDOC was significantly higher than HCR; paired *t*-test; $p < 0.05$). From March through September 1998, HCR clearly exceeded ΔDOC at all sampling sites (paired *t*-test; $p < 0.001$). During this period, DOC removal from porewater explained 36 ± 25 % of the concurrent oxygen consumption (Fig. 4).

Effects of temperature, VHG, and river DOC concentration on DOC immobilization and apparent oxygen consumption in the riparian zone

DOC removal from infiltrating water (ΔDOC) appeared to be largely unaffected by porewater temperature or VHG, although VHG and ΔDOC correlated at Stn D ($r = -0.793$; $p < 0.05$; Table 4). The relation between ΔDOC and river DOC concentrations (Fig. 3A) was highly site-dependent. While the DOC concentration of the river channel was strongly related to ΔDOC at Stn C ($r = 0.903$; $p < 0.001$), DOC immobilization was not related to DOC concentrations at the other locations (Table 4). Consequently, temperature, VHG, and river DOC concentration are poor predictors for ΔDOC, except at Stns C and D, where 83 and 74 %, respectively, of the variance in ΔDOC could be explained by temperature, VHG, and river DOC concentration (Table 5).

Hyporheic oxygen consumption was mainly related to porewater temperature (r always > 0.84; $p < 0.01$).

Table 4. Interaction of temperature, vertical hydraulic gradient (VHG), and DOC concentration in the infiltrating river water with DOC immobilization (ΔDOC) and oxygen consumption (ΔO_2) within the upper meter of the riparian zone. Pearson's correlation coefficients (of log-transformed data) are given for single stations and for pooled data from all stations. Levels of significance as in Table 3

Correlation	Correlation coefficient (r)				
	Stn C	Stn D	Stn E	Stn F	All stations
Temperature × ΔDOC	0.389	−0.297	−0.115	−0.020	−0.019
VHG × ΔDOC	−0.274	−0.793*	0.115	−0.226	−0.010
River DOC conc. × ΔDOC	0.903***	0.393	0.466	0.612	0.512**
Temperature × ΔO_2	0.863**	0.959***	0.840**	0.837**	0.701***
VHG × ΔO_2	0.070	0.520	0.651*	0.523	0.674***
ΔDOC × ΔO_2	0.466	−0.322	−0.094	0.119	0.148*
Counts	10	10	10	10	40

Table 5. Results of multiple regression analyses to predict DOC immobilization (ΔDOC) upon filtration of river water through the riparian zone (0 to 1 m). Independent variables (x_i) were entered in successive models. Standardized partial regression coefficients (β-coeff.; with level of significance of the associated *t*-value) are given for each independent variable. Levels of significance as in Table 3

Stn	β-coeff. (x_i)			Model R^2	p
(n)	River DOC conc.	VHG	Temperature		
C	0.903***			0.82	<0.001
(10)	0.887***	−0.068		0.82	0.003
	0.850*	−0.091	0.083	0.83	0.011
D	0.393			0.15	0.336
(10)	0.327	−0.765*		0.73	0.036
	0.351	−0.731	−0.068	0.74	0.117
E	0.466			0.22	0.244
(10)	0.476	−0.032		0.22	0.540
	0.587	0.267	−0.518	0.36	0.571
F	0.612			0.37	0.080
(10)	0.593	−0.152		0.38	0.219
	0.693	−0.041	−0.247	0.44	0.371
All stations	0.512**			0.26	0.002
(40)	0.512**	0.003		0.26	0.008
	0.615***	0.109	−0.281	0.32	0.007

Table 6. Results of multiple regression analyses to predict oxygen consumption (ΔO_2) upon filtration of river water through the riparian zone (0 to 1 m). Regression parameters and levels of significance as in Table 5

Stn (n)	β-coeff. (x_i) Temperature	VHG	ΔDOC	model R^2	p
C	0.863**			0.75	0.001
(10)	0.878**	−0.086		0.75	0.008
	0.815*	−0.036	0.139	0.77	0.026
D	0.959***			0.95	<0.001
(10)	0.920***	0.083		0.93	<0.001
	0.958**	0.026	−0.016	0.95	0.004
E	0.840**			0.71	0.002
(10)	0.706*	0.22		0.74	0.010
	0.870*	0.073	−0.003	0.85	0.043
F	0.837**			0.70	0.003
(10)	0.747**	0.229		0.75	0.008
	0.723**	0.366	0.216	0.87	0.011
All stations	0.701***			0.49	<0.001
(40)	0.520***	0.476***		0.69	<0.001
	0.569***	0.481***	0.164	0.78	<0.001

Interactions with other potentially important variables (VHG, ΔDOC) were less pronounced and generally not significant (Table 4). Temperature was a good predictor for interstitial oxygen consumption, explaining at least 70% of the variance in ΔO_2 (Table 6). Including VHG as an additional independent variable in multiple regression analysis led only to a slight increase of the model R^2 whereas ΔDOC as the third independent variable improved the model for Stns E and F ($R^2 = 0.85$ and 0.87, respectively).

Pooling apparent oxygen consumption data from all the stations, we found that apparent oxygen consumption was related to temperature and VHG (Fig. 5A, B), whereas no relation between ΔDOC and ΔO_2 was observed (Fig. 5C). However, linear regression of apparent oxygen consumption versus temperature yielded a much lower R^2 for pooled data ($R^2 = 0.49$) than for data from the individual stations (Table 6). As is evident from Fig. 5A, higher residual variance in the pooled ΔO_2 data resulted from significant differences in oxygen consumption between locations where natural sediment was present and those with artificially introduced filter material (Scheffé's test; $p < 0.05$). By including VHG as a predictor in multiple regression analysis, we found a significant improvement in model quality ($R^2 = 0.69$; Table 6). Altogether, temperature, VHG, and DOC immobilization explained 78% of the variance of the hyporheic apparent oxygen consumption (Table 6).

DISCUSSION

The sampling stations differed considerably from each other with respect to their hydraulic, geochemical, and biological characteristics (Figs. 2 to 4), particularly during the warm season (Table 2), possibly because low winter temperatures (Fig. 2A) limited the overall metabolic activity of the interstitial microorganisms.

Geohydrologic conditions

Hydraulic conductivity is generally higher in well-sorted sediments than in heterogeneous, poorly sorted sediments (e.g. Beyer 1964). Consistent with this, the *kf*-values obtained in this study indicate a higher permeability of the defined, artificially introduced filter material as compared to the original bank sediment (Table 1). Similarly, the VHG between the river channel and the subsurface depth layer was steeper at the stations with original sediment than at those within the artificially introduced gravel (Fig. 2C). In the near-surface layer, VHG varied over a wider range among the different stations than in the subsurface layer and was highest at Stn D (Fig. 2B). Generally, our VHG and *kf*-values indicate that deposition of fine suspended material (riverbed clogging) mainly occurred within the top sediment layer (i.e. within 10 cm from the sediment-water interface).

The temporal patterns of VHG and hydraulic conductivity indicate a general decline in the permeability of the bank sediments from October 1997 through April 1998 (Fig. 2, Table 1). Thereafter, VHG remained relatively constant throughout the warm season (May to September 1998), implying that the clogging of the sediment surface had reached a stable level, although small-scale spatial variations in hydraulic conductivity resulted in a considerable range of filtration velocity at Stn F (Table 1). The stations with artificially introduced gravel (Stns D and E) were apparently less affected by

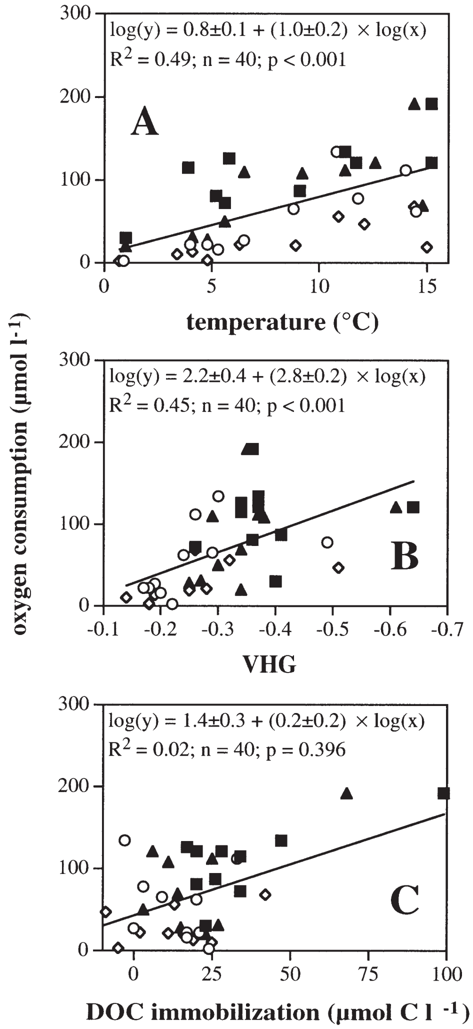

Fig. 5. Relation between apparent oxygen consumption during filtration through the riparian zone (within 0.9 to 1 m from the sediment-water interface) versus (A) temperature, (B) vertical hydraulic gradient (VHG), and (C) decrease in DOC concentration between river water and the subsurface sediment layer (DOC immobilization). Regression lines and equations refer to pooled data from all stations. Symbols represent Stns C (■), D (○), E (◇), and F (▲)

the clogging process than the stations with natural bed material (Fig. 2, Table 1).

The stations located within natural, undisturbed sediment showed higher abundance and production of porewater bacteria and a more pronounced decrease in oxygen concentration with distance from the water-sediment interface than the stations with the artificially introduced gravel (Fig. 3, Table 2). However, there were also several distinct differences between Stns C and F, suggesting that organic matter transformation and microbial activity were not only determined by the physical structure of the filter material. The DOC retention efficiency (defined as the amount of DOC immobilized during filtration divided by the amount of DOC that infiltrated from the river surface) ranged from 12 to 20% at the stations on the riverbank, but ranged from 29 to 38% at Stn C located on the riverbed (Fig. 4, Table 2). Similarly, apparent oxygen consumption was significantly higher at Stn C than at all the other stations, especially during the cold season (Table 2). Although information on the hydrologic conditions at Stn C is limited, hydrodynamic modelling (using the 'modflow' transport model) provides evidence that the riverbed contributed only little (<10%) to the transport of river water to the production well (Ingerle et al. 1999). If downstream subsurface flow prevailed over downwelling of river water into the sediment at Stn C, this would imply a higher HRT at this site and differences in the sources of organic matter between the riverbed and the sites located on the riverbank.

Importance of DOC immobilization for the microbial metabolism in the hyporheic zone

Removal of DOC from interstitial waters is often linked to the abundance and the activity of hyporheic bacteria (Findlay et al. 1993, Marmonier et al. 1995) and bacterial growth on porewater DOC has been demonstrated (Findlay et al. 1993, Mann & Wetzel 1995). However, abiotic immobilization (via the diffusion of solutes into the biofilm matrix of sediments and adsorption onto biofilm binding sites and mineral surfaces) is considered to be an important mechanism in the removal of DOC from interstitial waters (McDowell 1985, Fiebig & Lock 1991). Findlay & Sobczak (1996) reported that DOC immobilization in bed-sediments of a nutrient-rich 3rd order stream (Wappinger Creek, USA) was only weakly correlated with temperature and oxygen consumption, but depended strongly on streamwater DOC concentration. In our study, the instantaneous bacterial utilization of the infiltrating DOC is only of minor importance for the removal of DOC as indicated by the weak correlation between DOC immobilization (ΔDOC) and concurrent oxygen consumption (Table 4, Fig. 5C). In contrast to earlier reports (McDowell 1985, Findlay & Sobczak 1996), however, there was no clear relationship detectable between ΔDOC on the riverbank and the DOC concentration of the infiltrating river water (Table 4). We assume that adsorption processes were more pronounced on the riverbed than at the stations located on the riverbank. The higher DOC retention observed at Stn C compared to the other sampling sites (Fig. 4) may have been the result of abiotic immobilization processes rather than caused by spatial differences in microbial activity.

Most of the DOC in natural waters is not readily available for bacteria (e.g. Thurman 1985). For the period of the investigation, 2 to 29% of the DOC found in the Enns River can be regarded as bioavailable DOC (Kolar et al. unpubl.). The measurements of Kolar et al. (unpubl.) may actually underestimate the bioavailability of the infiltrating DOC as scavenging of molecules within the sediment biofilm may allow the utilization of compounds that otherwise would not be accessible for bacterial degradation (Freeman & Lock 1995, Findlay & Sobczak 1996). However, even if we assume that the observed decline in DOC is exclusively attributable to microbial consumption, the observed losses of DOC were frequently lower than the apparent microbial respiration (in terms of carbon equivalents; Fig. 4). This discrepancy between the removal of DOC and oxygen from infiltrating river water was generally more pronounced at the stations with natural bed material than at those with artificially introduced gravel, but was observed at all sites from April to September 1998 (Fig. 4). During this period, DOC removal from porewater explained 36 ± 25% (mean ± SD) of the variance in the apparent oxygen utilization. Our results are in good agreement with earlier observations, where the loss of DOC accounted for 24 to 39% of the concurrent oxygen depletion (Findlay et al. 1993).

The imbalance between ΔDOC and HCR observed in our study (Fig. 4) strongly suggests that carbon sources other than infiltrating DOC contributed substantially to microbial demand. Recently, we proposed that POC may be the predominant carbon source for microbial metabolism because total bacterial biomass and production were highly correlated with the distribution of sediment-associated organic carbon (Brugger et al. in press).

Factors determining the microbial oxygen consumption in the riparian zone

Temperature is a major factor determining the metabolism of organic matter and biological activity in hyporheic habitats (e.g. Brunke & Gonser 1997). Seasonal temperature variations have been demonstrated to influence the abundance and the production of bacteria in our system (Brugger et al. in press), and temperature alone explained >70% of the seasonal variability in apparent oxygen consumption (Table 6). However, porewater temperature differed only slightly between the individual sampling sites at a given date (Fig. 2A) and is therefore not likely to be responsible for the observed spatial heterogeneity in the interstitial bacterial abundance, production, and oxygen consumption (Figs. 3 & 4).

The residence time of the infiltrating water can also influence the interstitial oxygen consumption of the riparian zone. Findlay (1995) argued that the residence time of water in the hyporheic zone may explain the variability in oxygen distribution among streams, because the breakdown of interstitial organic matter depends largely on the duration of interaction between the organic material and the sediment biofilm. Based on the available filtration velocity data (Table 1), we calculated HCR rates (per infiltration area and unit time) for the investigated system. Because filtration velocity was averaged over the period of investigation in these calculations, these data represent only rough estimates of the hyporheic community respiration rates. HCR rates at Stn D ranged from ~30 mmol C m^{-2} d^{-1} (during the cold season) to ~110 mmol C m^{-2} d^{-1} (during the warm season). In comparison, HCR rates of ~30 mmol C m^{-2} d^{-1} (cold season) and ~60 mmol C m^{-2} d^{-1} (warm season) were obtained for Stn F. Therefore, once the longer residence time of the infiltrating water at Stn F was taken into account, community respiration was similar or even higher in the artificially introduced gravel compared to the original bank sediment. These results are consistent with the findings of Jones (1995) from bed-sediments of a small desert stream (Scyamore Creek, USA), where microbial oxygen consumption was inversely correlated with the sediment grain size. Calculated per sediment surface area, Jones (1995) found a more than 4-fold higher oxygen consumption rate for sediments with a mean particle diameter of 3.4 mm as compared to smaller sized (0.5 mm) sediments. The author explained the higher respiration in the coarser sediments by the higher interstitial flow rate and by potentially higher diffusive transport of oxygen within the sediment biofilm.

Overall, the apparent community respiration rates obtained in this study are within the range of published data. For example, Grimm & Fischer (1984) reported a community respiration rate of 106 mmol C m^{-2} d^{-1} from shallow bed-sediments of Scyamore Creek and rates of ~50 mmol C m^{-2} d^{-1} were determined in surface sediments of a 3rd order mountain stream (Steina, Germany; Fischer et al. 1996, Pusch 1996).

Role of bacteria for DOC immobilization and oxygen consumption in the riparian zone

Porewater bacterial metabolism (Fig. 3D) accounted for less than 1% of the respiration-based community carbon consumption (assuming a bacterial growth efficiency of 10%; cf. Mann & Wetzel 1995). This is consistent with previous observations that porewater bacteria represented <1 % of the total bacteria present in the investigated system (Brugger et al. in press) and suggests that porewater bacteria do not play a significant role in the cycling of the interstitial organic carbon. We cannot directly compare the bacterial production rates obtained in this study with rates of sediment-associated bacterial production, because bacterial production in Brugger et al. (in press) was expressed on the basis of sediment dry mass and the conversion into area-based production rates would require assumptions regarding the specific weight of the undisturbed sediment. However, hyporheic community respiration at Stn F correlated well ($r = 0.682$; $n = 10$; $p < 0.05$) with the sediment-associated bacterial production rates given in Brugger et al. (in press), supporting Pusch's (1996) argument that most of the oxygen removal in interstitial zones can be attributed to sediment-attached bacterial respiration.

Porewater bacterial abundance and production is not related to the distribution of DOC and oxygen within the riparian zone (Table 3). Thus, bacterial parameters were not included in models predicting DOC immobilization or oxygen consumption (Tables 5 & 6). As indicated by the calculated area-based HCR rates, high bacterial abundance and production in the porewater of the shallow sediment layers of Stns C and F (Fig. 3C,D) do not necessarily reflect an overall higher bacterial activity in the original sediment compared to the artificially introduced gravel (Fig. 4). The accumulation of porewater bacteria near the sediment-water interface as well as the sharp decreases in bacterial abundance during the first meter of filtration (Fig. 3C) resulted probably from a combined effect of adsorption of bacteria and labile DOC onto the interstitial surfaces (e.g. Lawrence et al. 1995).

Summary

In the present paper we demonstrated that substantial amounts of oxygen were consumed in waters entering an experimental bank filtration site. Sediment-associated rather than interstitial bacteria were responsible for the observed decline in oxygen concentration via the utilization of POC and DOC. The activity of the free-living, interstitial microorganisms was highly temperature-dependent, but was not related to the amount of DOC immobilized during filtration. Furthermore, the immobilization of DOC from infiltrating water was significantly lower than the concurrent oxygen decline. The physical structure (i.e. the grain size distribution) of the riparian sediments controlled the flux of water and solutes into the riparian zone, and hence determined the relative importance of POC and DOC as carbon sources for the hyporheic organisms. Filtration velocity and hydraulic residence time of the infiltrating water were, however, not the major factors determining the area-based community respiration rate.

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